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Effects of abiotic conditions and microarthropod predation on the structure and function of soil animal communities

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Two experiments were established to compare the relative importance of biotic (predation) versus abiotic factors affecting the soil animal community structure and the nutrient dynamics in microcosms simulating coniferous forest soil. The experiments had either a diverse or greatly reduced assemblage of soil fauna as the prey community, both with and without mesostigmatid mites as predators. The experiments were carried out in the field, and under two different laboratory conditions: 1) at a constant temperature and 2) at varied temperature and illumination regimes simulating field conditions. Two destructive samplings were performed, including analysis of numbers and composition of the soil fauna and measurement of KCl-extractable NH_4^+-N and PO_4^{3-}-P in the test materials. In the second experiment soil respiration was measured weekly, as well. Abiotic conditions had stronger effects on modifying the structure of soil animal communities and nutrient dynamics than predators. Nevertheless, mesostigmatid mites as predators proved to be an important group affecting the arthropod community in each abiotic environment, although the impact of predators differed between the abiotic conditions. The results show abiotic and biotic factors to possess complex mutual interrelationships, emphasizing the difficulty of applying laboratory data to field conditions. Laboratory experiments with too simple faunal composition may overemphasize the role of a small group of soil animals in ecosystem functioning.

1. Introduction

The relative importance of biotic versus abiotic factors modifying community organisation has received considerable attention in the ecological literature. Numerous experiments exist in which the effects of either a biotic or an abiotic factor have been tested, but studies which take account of both factors are rare. Since the outcome of biotic interaction is usually dependent on abiotic factors (Begon et al. 1990), one cannot simply state that abiotic conditions are merely a background against which species interactions are played out (Dunson 1991).

Below ground communities, representing systems being inseparably modified by biotic and abiotic factors (Swift et al. 1979, O'Neill et al. 1986) have received less interest than above ground food webs. This may be due to the opaque nature of soil communities with a great number and diversity of soil organisms. However, in many cases predation and grazing on soil microbes has been recorded as dramatically affecting the prey populations, leading to changes in ecosystem level processes, for instance in the decomposition rate (see e.g. McCellan et al. 1981, Clarholm 1985, Brussaard et al. 1991, Setälä et al. 1991). Moreover, predation of nematodes by arthropods or predaceous nematodes has also been shown to affect nutrient dynamics in some laboratory experiments (e.g. Setälä et al. 1991). However, predation on microarthropods and its possible consequences on below ground processes has received far less attention, despite the great number and functional diversity of this group in detrital food webs. In other words, the "level" at which functional top-down regulation generally takes place has been assumed to be situated close to the base of the food web (microbes exploiting dead organic matter, or in the next higher level with fauna grazing on microbes).

We established two microcosm experiments to explore whether varying abiotic conditions affect the structure and function of relatively diverse soil animal communities, and whether biotic factors (predation on a microarthropod level) exert a different impact on these variables in abiotically different conditions.

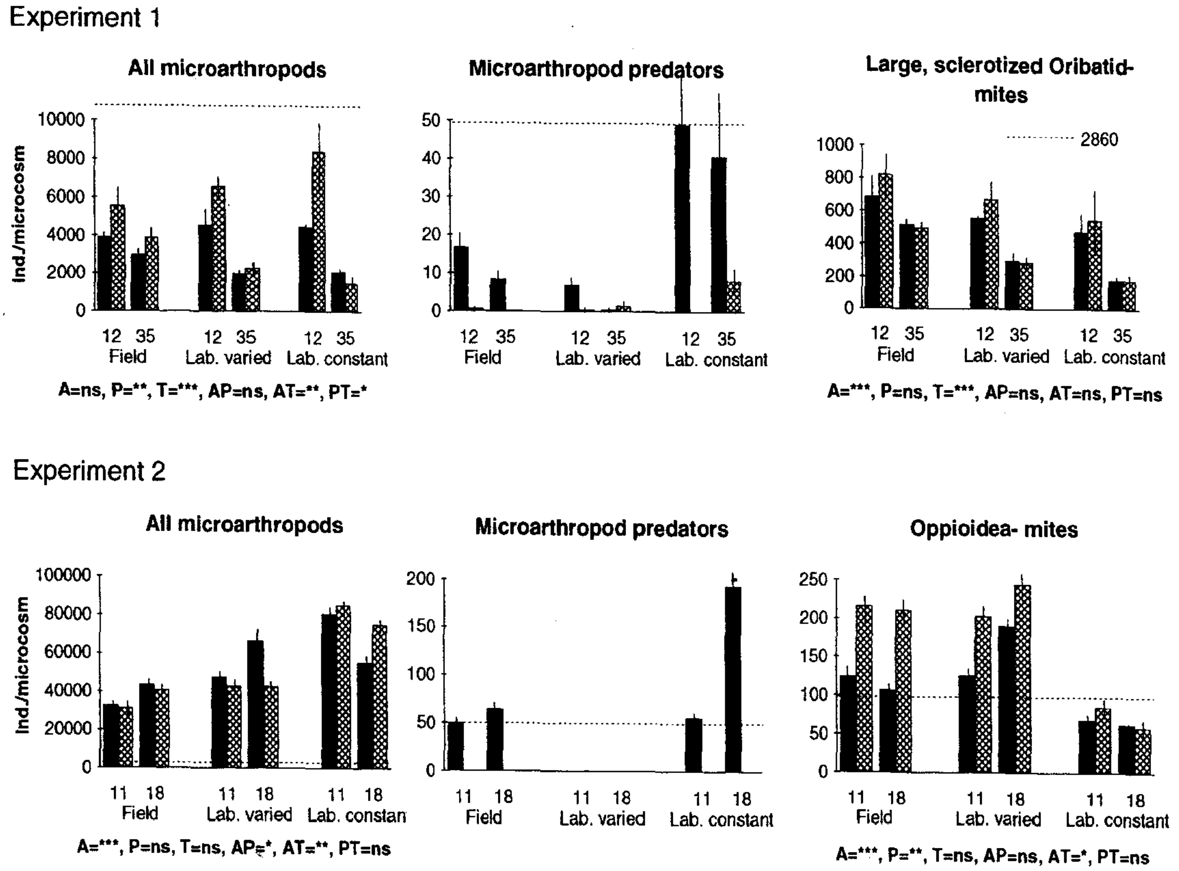

Fig. 1. Numbers of microarthropods (ind./microcosm ± *SE*) in the humus and litter layers in destructive samplings. Solid bars are for treatments with predators and hatched bars for treatments without predators. - - - - - - - = number of arthropods at week 0. Results of factorial ANOVA indicated under the graphs as follows: A = abiotic, P = predator, and T = time factor; * = $P < 0.05$, ** = $P < 0.01$ and *** = $P < 0.001$.

2. Materials and methods

Two microcosm experiments were designed to study the effects of three abiotic conditions (field, laboratory constant and laboratory varied), two biotic compositions (predator/non-predator) and their interactions on the structure of soil animal communities, and on the leaching of N and P indicating the function of these communities. The experiments lasted 240 (Exp. 1 16.08.1990–19.04.1991) and 120 (Exp. 2 28.06.1991–4.11.1991) days. Both experiments were carried out in the field (microcosms partly buried in coniferous forest floor) and under two different laboratory conditions: at constant temperature (+16±1°C, in darkness) and at varied temperature and illumination regimes simulating field conditions.

Plastic containers (vol. 1.8 l for Field and 2.2 l for Laboratory, area 154 cm^2) were used in both experiments. In the field the bottom and top of the microcosms were closed with 48 µm nylon mesh, whereas in the laboratory the containers were otherwise closed systems but had a small hole in the lid to allow gas exchange. The test materials (litter, humus and mineral soil from coniferous forest) were defaunated using liquid nitrogen (humus and litter) or washing with hot water and freezing at –20°C (mineral soil). After defaunation the materials were introduced to the microcosms to form a layered soil structure (layer thickness 1, 3 and 2.5 cm in litter, humus and mineral soil, respectively). A natural inoculum of microbes, nematodes and tardigrades was added in a water suspension to the test materials (for methods see Huhta & Setälä 1990), whereafter the microcosms received an arthropod prey community with or without 50 individuals of mesostigmatid mites known to feed on microarthropods (e.g. Wallwork 1970 and Karg 1971).

Experiment 1 had a diverse and abundant soil fauna as a prey community from the beginning of the experiment, the community being dominated by oribatid mites (Appendix 2). In half of the microcosms *Pergamasus lapponicus, P. brevicornis, Vulgarogamasus kraepelini, Veigaia nemorensis* and *Hypoaspis aculeifer* (total 50 individuals/microcosm) were used as predators. The fauna was obtained with several dry funnel extractions from topsoil material (the predators and macrofauna were manually removed from the prey community).

Experiment 2 had a simple prey community consisting of four species of Oribatid mites and four species of Collembola obtained from laboratory cultures (see Appendix 2). *Pergamasus brevicornis* (10 individuals) and *Veigaia nemorensis* (40 individuals) were used as predators in half of the microcosms.

Two destructive samplings were performed for both experiments (at weeks 12 and 35 for Exp. 1 and at weeks 11 and 18 for Exp. 2), including the analysis of numbers and composition of the fauna, and photometrical determination of KCl-extractable NH_4^+ and PO_4^{3-} (for methods, see Haimi & Huhta 1990) in the test materials. In experiment 2 soil respiration was measured weekly. Factorial ANOVA was used for analysing the results (predator treatment, abiotic condition and sampling time as factors). The number of replicates in each treatment combination was five for both experiments.

3. Results

3.1. Effects of abiotic factors on fauna and system functioning

The development of microarthropod (Fig. 1) and nematode populations (Table 1 and Appendix 1) was significantly affected by abiotic conditions in both experiments. In Experiment 1 dominating microarthropod groups were different in each abiotic environment: in the Field adult *Tectocepheus* and *Conchogneta* mites and small (<0.4 mm) juvenile Oribatid mites were most abundant, whereas in the laboratory conditions generally more juvenile stages of Oribatid mites were found. Simpson's diversity index for arthropods was lower in laboratory conditions than in the Field (Table 2 and Appendix 1). In Exp. 2 more than 90% of all microarthropods consisted of *Folsomia candida* and *F.*

Table 1. Number of nematodes (ind./g d.m. ± *SD*) in humus and litter layers in microcosms incubated in three abiotic environments in the presence (with) or absence (without) of predatory mites in Experiments 1 and 2.

	Field		Laboratory (Varied)		Laboratory (Constant)	
	with	without	with	without	with	without
Experiment 1						
Week 12	387 ± 222	517 ± 172	313 ± 152	168 ± 44	1422 ± 994	2284 ± 1490
Week 35	765 ± 297	624 ± 172	732 ± 406	669 ± 282	251 ± 200	193 ± 126
Experiment 2						
Week 11	2685 ± 650	1599 ± 519	443 ± 91	396 ± 202	1022 ± 265	998 ± 417
Week 18	1090 ± 642	823 ± 608	421 ± 304	258 ± 207	1286 ± 402	1573 ± 567

Table 2. Simpson's diversity index (mean ± *SD*) for microarthropod communities in three abiotic conditions in the presence or absence of predatory mites at weeks 12 and 35 in Experiment 1. The index was calculated for each separately counted arthropod group (see Appendix 1).

	Field		Laboratory (Varied)		Laboratory (Constant)	
	with	without	with	without	with	without
Week 12	9.95 ± 2.10	9.21 ± 1.70	9.25 ± 1.90	5.31 ± 1.89	8.24 ± 0.535	7.76 ± 1.54
Week 35	10.18 ± 1.27	11.37 ± 1.34	4.09 ± 0.72	8.86 ± 5.78	6.13 ± 2.96	7.14 ± 2.36

Table 3. Amount of KCL-extractable NH_4^+ -N in humus and litter layers and PO_4^{3-} -P in mineral layer (μg/g d.m. ± *SD*) in three abiotic environments with or without predatory mites in Experiments 1 and 2.

	Field		Laboratory (Varied)		Laboratory (Constant)	
	with	without	with	without	with	without
Experiment 1						
NH_4^+ -N, week 12	345 ± 41	350 ± 29	352 ± 30	411 ± 33	525 ± 20	534 ± 48
NH_4^+ -N, week 35	406 ± 39	383 ± 54	243 ± 34	222 ± 33	442 ± 223	393 ± 62
Experiment 2						
NH_4^+ -N, week 11	94 ± 13	145 ± 18	312 ± 34	379 ± 29	433 ± 59	430 ± 54
NH_4^+ -N, week 18	52 ± 8	67 ± 29	292 ± 27	346 ± 46	497 ± 29	494 ± 18
PO_4^{3-} -P, week 11	0.90 ± 0.30	1.4 ± 0.50	0.78 ± 0.10	0.88 ± 0.40	0.64 ± 0.17	1.04 ± 0.46
PO_4^{3-} -P, week 18	0.02 ± 0.00	0.05 ± 0.02	0.04 ± 0.03	0.02 ± 0.02	0.05 ± 0.08	0.06 ± 0.05

fimetaria in each abiotic treatment. In the Field and in Varied laboratory conditions (both with relatively low temperatures) generally less microarthropods were recorded than in Constant temperature conditions (Fig. 1). In both experiments the number of predators were smallest in Varied and highest in Constant laboratory conditions. In Exp. 2 predators became extinct in the Varied laboratory conditions before the first destructive sampling at week 11.

In both experiments the mobilisation of NH_4^+ and PO_4^{3-} was strongly affected by abiotic conditions (Table 3, Appendix 1), the effect being different depending on the experiment. Soil respiration in microcosms in Constant laboratory conditions was higher than in the Field and Varied laboratory conditions in Exp. 2 (Table 4).

3.2. Effects of predators on prey populations and system functioning

In Exp. 1 predators reduced the total number of microarthropods in the Field and Constant laboratory conditions. However, predators had no significant effect on the numbers of adult, hard-bodied Oribatid mites, which were numerous in each treatment (Fig. 1). Despite the predator induced changes in the prey community, nutrient dynamics did not differ between predated and nonpredated systems (Table 3, Appendix 1).

In Exp. 2 predators had complex effects on their prey populations, the effects being dependent on the abiotic environment and taxonomic group in question. In systems with predatory mites, the numbers of Collembola decreased in Constant laboratory conditions but increased in Varied laboratory conditions. In the Field numbers of Oppioidea mites were significantly reduced when predators were involved (Fig. 1). In the presence of predators mobilisation of NH_4^+ (in humus and litter) and PO_4^{3-} (in mineral layer) was reduced in the Field and Varied laboratory conditions as compared to systems without microarthropod predators (Table 3 and Appendix 1). Mesostigmatid mites did not affect the respiration rate in the microcosms significantly (Table 4).

4. Discussion

In both experiments the development of faunal communities was affected more clearly by the abiotic environment than by biotic relationships between the predators and the prey. This was also the case with mineralisation of N and P. Since the average temperature, distribution of moisture between soil layers within a system and illumination [all these factors known to affect soil biota and decomposition significantly (e.g. Swift et al. 1979)] differed between abiotic treatments, the result is not surprising. It is difficult, however, to draw conclusions about the relative importance of the individual abiotic factors bringing about the differences between the treatments. Still, we may assume that the dryness of the litter layer in microcosms of Varied laboratory conditions most probably caused the decline in predator numbers in both experiments and decreased the diversity of microarthropods in Exp. 1. In Constant laboratory conditions the absence of natural temperature and light periodicity may have prevented the completion of life cycles and excluded some species. In addition, the low number of microarthropods and nematodes at week 35 and the relatively high respiration rate of Constant laboratory conditions in Experiment 1 indicate resource depletion and thus intense competition which may have also lowered diversity. Hutchinson (1961) pointed out that the absence of stochastic fluctuations may decrease diversity by increasing the rate of competitive exclusion. Unpredictable fluctuations may not only slow down competitive exclusion, but can also form a strong mechanism of coexistence together with non-linear population dynamics and overlapping generations (Chesson 1986). According to these views, the very stable environmental conditions (i.e. low degree of stochastic fluctuations) in the laboratory as compared to the field may partly explain the higher diversity of microarthropods in the field microcosms.

The predators seemed to affect nutrient dynamics only in Exp. 2 with a structurally simple prey community in which the majority of the prey fauna was composed of Collembola. In Exp. 1, on the other hand, the more complex microarthropod community consisted mainly of strongly sclerotized Oribatid mites. We assume that the absence of a significant functional response to predator treatment in Exp. 1 was due to a large proportion (both in biomass and numbers) of strongly sclerotized Oribatid mites capable of avoiding predation (Walter et al. 1988). It is also notable that the initial composition of the fauna differed between the two experiments; in Exp. 2 the predator to prey ratio was larger than that of Exp. 1, allowing predators to exert stronger effects on prey communities already at the beginning of Exp. 2.

Despite the fact that the impact of predation on microarthropods and system functioning differed between the abiotic treatments, mesostigmatid mites proved to be an important group affecting the arthropod community in each abiotic environment. A somewhat unexpected increase in collembolan numbers in initially predated systems (all predators died before week 11) in Varied laboratory conditions of Exp. 2 remains unexplained, because the population size of Collembola was measured only twice during the experiment. However, the increase cannot account for differences in the size structure of the populations since

Table 4. Cumulative soil respiration (mg C/g d.m.) during weeks 0–18 in microcosms with or without predatory mites in three abiotic treatments in Experiment 2.

	Field		Labor. (Varied)		Labor. (Const.)	
	with	without	with	without	with	without
mg C	106.0	106.1	92.6	89.7	145.5	148.5
Average temp.	10°C		13°C		16°C	

the individual collembolans were of equal size in both biotic treatments (results not shown).

Many studies on species interactions have been performed with communities having an unnaturally simple biotic structure (Walter et al. 1989). However, the properties of a simplistic "food chain system" are likely to be different from more complex "food web systems" (Pimm 1982). A removal of a single species or a relatively small functional group may alter system functioning more in simple communities than in complex multi-species communities, in which the effect of species removal may be buffered by other unaffected members of the same functional group. To conclude, differences in the properties of simple and complex animal communities emphasize the need of studies with complex, natural biota. This is particularly true in below ground systems in which our current knowledge on trophic behaviour is largely based on investigations on a few well-studied taxa.

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Appendix 1. Tables of variances (factorial ANOVA) for nematode numbers, amounts of KCl- extractable nutrients and for Simpson's diversity index for microarthropods. All interactions with three factors were non-significant. * = Bartlett-Box or Cochran's C tests were significant at < 0.05 level, indicating nonhomogenous variances between treatments.

Variables	Factors:	Abiotic (A)	Predators (P)	Time (T)	A x P	A x T	P x T
Experiment 1							
Nematodes, humus and litter layers		n.s.	n.s.	n.s.	n.s.	0.000	n.s.
Ammonium, humus and litter layers		0.000	n.s.	0.001	n.s.	n.s.	n.s.
Diversity		0.000*	n.s.	n.s.	n.s.	0.010*	n.s.
Experiment 2							
Nematodes, humus and litter layers		0.000	n.s.	0.017	n.s	0.001	n.s.
Ammonium, humus and litter layers		0.000*	0.001*	n.s.	0.019*	0.000*	n.s.
Phosphate, mineral layer		n.s.	0.010	0.000	n.s.	0.042	0.026

Appendix 2. Composition of microarthropod prey communities at the beginning of Experiments 1 and 2 (week 0). In Experiment 1 the numbers of microarthropods (ind./microcosm ± S.D) are based on a 3% subsample from each microarthropod inoculum.

	Experiment 1		
Mesostigmata, Gamasina		*Porobelba spinosa* (Selln.)	7.77 ± 14.2
Parazercon radiatus Berlese	46.6 ± 22.9	*Belba verrucosa* B.-Z.	1.04 ± 1.71
Eviphis ostrinus ad. (C.L.K.)	2.48 ± 3.81	*Tectocepheus velatus* Mich.	1400 ± 619
juv.	0.31 ± 1.18	*Chamobates voigtsi* (Oudemans)+ *C. spinosus* Sellnick+ *Ceratozetella thienemanni*(Willmann)	1630 ± 666
Uropodina		*Parachipteria willmanni* Hammen	43.5 ± 21.7
Urodiaspis tecta ad. (Kramer)	5.39 ± 7.56	*Eupelops torulosus* (C. L. Koch)	217 ± 162
juv.	1.91 ± 2.36	*Carabodes forsslundi* Sellnick ad.	36.5 ± 36.1
Trachytes spp. ad.	21.6 ± 12.3	juv.	59.9 ± 53.1
juv.	7.23 ± 5.1	*Liacarus coracinus* C. L. Koch	42.6 ± 35.7
Ipiuropoda dialveolata Hirscm. & Zirng, Nicol.	17.3 ± 16.5	*Xenillus tegeocranus* Hermann	0.86 ± 3.30
Dinychus perforatus Kramer 1882	1.30 ± 4.00	*Adoristes poppei* Oudemans	205 ± 95.8
Uropodina ad.	0.43 ± 2.37	*Hypoctonius rufulus* C. L. Koch ad.	20.4 ± 16.9
juv.	3.38 ± 4.94	juv.	10.5 ± 7.78
Oribatei, Macropylina		*Platynothrus septentrionalis* Sellnick	11.2 ± 9.87
Nothrus silvestris Nicolet ad.	215 ± 102	Oribatida	79.4 ± 81.8
juv.	313 ± 135	Oribatida juv. 1(> 0.40 mm)	168 ± 128
Nothrus palustris C.L. Koch ad.	3.03 ± 6.55	Oribatida juv. 2(< 0.40 mm)	1150 ± 732
juv.	37.3 ± 32.2	Prostigmata	2.41 ± 4.43
Heminothrus paolianus Berlese	20.5 ± 13.2	Scutacridae	10.6 ± 19.1
Heminothrus punctatus C. L. Koch	81.1 ± 27.4	Astigmata	0.32 ± 1.29
Heminothrus juv.	418 ± 147	Collembola	
Nanhermannia sellnicki Forsslund	39.0 ± 20.6	*Folsomia quadrioculata* Tullberg ad.	80.5 ± 93.6
Steganacarus carinatus C L Koch ad.	53.9 ± 26.1	juv.	2.61 ± 5.57
juv.	101 ± 42.0	*Isotoma hiemalis* Schött ad.	14.5 ± 13.0
Phtiracarus longulus (C. L. Koch) ad.	1.70 ± 1.98	juv.	7.83 ± 29.3
juv.	59.4 ± 36.1	Isotomidae	29.5 ± 42.9
Macropylina juv. 1(> 0.40 mm)	22.6 ± 15.7	*Willemia cf. anophtalma* (Börner)	5.92 ± 5.22
Macropylina juv. 2(< 0.40 mm)	126 ± 90.8	*Neanura muscorum* (Templeton)	1.01 ± 1.97
Brachypylina		*Tomocerus flavescens* (Tullberg)	1.03 ± 4.15
Oppiella nova (Oudemans)	1140 ± 522	*Tomocerus spp.*	0.69 ± 2.62
Lauroppia translamellata (Willmann)	873 ± 615	Homoptera, Coccoidea	8.29 ± 11.7
Medioppia subpectinata (Oudemans)	475 ± 306	Thysanoptera	6.50 ± 10.7
Conchogneta trägårdhi (Forsslund)	746 ± 461	Diptera	
Suctobelbidae	670 ± 362	Nematocera (larva)	0.28 ± 0.91
Oppioidea	6.31 ± 30.8	Brachycera + Cyclorrhapha (larva)	3.01 ± 3.25
	Experiment 2		
Total numbers of Collembola	150	Total numbers of Oribatida (Oppioidea)	100
Species composition (exact numbers):		Species composition (estimated numbers):	
Folsomia candida (Willem)	25	*Oppiella nova* (Oudemans)	26
F. fimetaria (Linne)	25	*Medioppia subpectinata* (Oudemans)	48
Isotoma notabilis Shäffer	50	*Conchogneta trägårdhi* (Forsslund)	19
Willemia cf. anophtalma Börner	50	Suctobelbidae	7